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Cyanobacteria vs green algae: which group has the edge?

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The dogma surrounding carbon assimilation has it that, due to their highly effective CO₂-concentrating mechanisms, cyanobacteria will always out-perform, for example, green algae where inorganic carbon is in short supply. Working on the cyanobacterial genus *Microcystis*, Ji *et al.* (2017) now suggest this might not always be true, with possible improved performance with rises in atmospheric (and hence dissolved) CO₂. Many cyanobacteria form extensive toxic blooms that present significant health risks and economic costs: how they will react in a future world with elevated CO₂ and temperature is thus of intense interest for water management.

Cyanobacteria and algae possess various inorganic carbon transporters (CO₂-concentrating mechanisms, CCMs) that serve to increase the CO₂ concentration at the active site of Rubisco (ribulose-1,5-bisphosphate carboxylase oxygenase). CCMs presumably evolved because the CO₂-fixing enzyme has a relatively low catalytic rate and expresses a competitive oxygenase as well as the carboxylase activity, with the rates of the two activities depending on the O₂:CO₂ ratio at the active site of the enzyme, according to Eqn (1):

$$S_{\text{rel}} = [K_{0.5}(\text{O}_2) \cdot k_{\text{cat}}(\text{CO}_2)] / [K_{0.5}(\text{CO}_2) \cdot k_{\text{cat}}(\text{O}_2)] \quad (1)$$

where the selectivity factor S_{rel} defines the ratio of rates of carboxylase to oxygenase reactions, $k_{\text{cat}}(\text{CO}_2)$ = CO₂-saturated specific rate of carboxylase activity of Rubisco (mol CO₂ mol⁻¹ active site s⁻¹), $K_{0.5}(\text{CO}_2)$ = concentration of CO₂ at which the CO₂ fixation rate is half of $k_{\text{cat}}(\text{CO}_2)$, $k_{\text{cat}}(\text{O}_2)$ = O₂-saturated specific rate of oxygenase activity of Rubisco (mol O₂ mol⁻¹ active site s⁻¹) and $K_{0.5}(\text{O}_2)$ = concentration of O₂ at which the O₂ fixation rate is half of $k_{\text{cat}}(\text{O}_2)$.

A number of different forms of Rubisco, with a range of kinetic properties, occur in autotrophic organisms (Badger *et al.*, 1998; Raven and Beardall, 2003; Beardall and Raven, 2016). In short, freshwater cyanobacteria tend to have Rubiscos with high $K_{0.5}(\text{CO}_2)$ and k_{cat} , and low S_{rel} values whereas green algae have Form 1B Rubiscos with higher affinity [lower $K_{0.5}(\text{CO}_2)$] and S_{rel} but lower k_{cat} (Raven and Beardall, 2003). Differences in the kinetic properties of Rubisco among species mean that the different forms of

Rubisco will perform differently at a given set of CO₂ and O₂ concentrations at the active site. Thus, at present-day dissolved CO₂ levels, organisms with low affinity for CO₂ [high $K_{0.5}(\text{CO}_2)$] will have Rubiscos operating well below maximum capacity if internal CO₂ is in equilibrium with (or lower than) external CO₂; indeed, species such as dinoflagellates, with their low S_{rel} Form II Rubisco would probably be incapable of performing net C assimilation with diffusive CO₂ entry at air equilibrium (Beardall and Raven, 2016). Although some algal species are capable of functioning well with diffusive CO₂ entry, these tend to be restricted to environments where CO₂ levels are high – as is the case for the freshwater red algae belonging to the Batrachospermales (Raven *et al.*, 1982), the Chrysophytes *sensu lato* (Maberly *et al.*, 2009), and the coccoid symbiotic green alga *Coccomyxa* using CO₂ from soil or basiphyte respiration (Raven and Colmer, 2016) – or where low light levels constrain photosynthesis so CO₂ diffusion is sufficient to satisfy demand (Kübler and Raven, 1994, 1995). In all other cases examined, net CO₂ assimilation by cyanobacteria and algae requires the operation of a CCM, which increases the CO₂ supply to the active site of Rubisco.

Not all CCMs are equal

In general terms, and as a consequence of the lower affinity of their Rubiscos for CO₂, cyanobacteria tend to show higher expression of CCM activity (based on internal:external CO₂ concentration ratios) compared to green algae and this, together with observations of preferences of cyanobacteria for high pH environments where the proportion of CO₂ relative to bicarbonate is low, is taken as suggesting a greater competitive ability by cyanobacteria when CO₂ levels are low. As pointed out by Ji *et al.* (2017), there is some evidence for this from ecological observations (Shapiro, 1990, 1997) as well as previous competition experiments with freshwater phytoplankton communities (Low-Décarie *et al.*, 2011, 2015), though Caraco and Miller (1998) caution that high pH could be as important a driver to the competitive success of cyanobacteria as CO₂.

Such generalizations, however, tend to ignore the variability among CCMs and specifically the range of transporters used for inorganic carbon acquisition. Thus cyanobacteria

can express up to five different transporters of inorganic carbon with differing capacity, substrates and affinity. These are summarized in [Box 1](#).

What is also apparent in a number of systems is that in addition to physiological plasticity within a given strain, there is also genetic heterogeneity within cyanobacterial strains of the same species. In the case of *Microcystis* responses to light, for instance, [Kardinaal et al. \(2007\)](#) suggested that the shift from toxic to non-toxic strains during blooms can be explained by a difference in their ability to compete for light. For inorganic carbon use, [Sandrini et al. \(2014, 2015\)](#) and [Visser et al. \(2016\)](#) have shown that, for a number of cyanobacterial genera and species, strains exist that express genes for different combinations of the five transport systems shown in [Box 1](#). Given that these different transporters confer different properties related to inorganic carbon uptake under different CO₂/HCO₃⁻ concentrations, different strains might be expected to respond differently to changes in CO₂ levels. This expectation was recently confirmed. [Sandrini et al. \(2016\)](#) showed, in selection experiments and a lake study, that the strain composition of *Microcystis* adapts to rising CO₂ levels. Natural selection favours *bicA* + *SbtA* strains in dense blooms in which CO₂ is depleted, while *bicA* strains benefit from high CO₂ concentrations. The CCMs of green algae have not been as extensively characterized as those of cyanobacteria, but, in general, accumulation factors (CO₂ in:CO₂ out) for chlorophytes are much lower ([Raven and Beardall, 2003](#)). This does not necessarily make them poor performers at low CO₂ as the K_{0.5} (CO₂) for their Rubiscos is lower than that of cyanobacteria.

This is where the work reported by [Ji et al. \(2017\)](#) comes in. They took a strain of the toxic cyanobacterium *Microcystis* which expresses *bicA*, a low affinity, high flux transporter ([Box 1](#)), and three green algal species, *Scenedesmus obliquus*, *Monoraphidium griffithii* and *Chlorella vulgaris*, and grew them in monoculture and then in various combinations in competition at low (100 ppm) and high (2000 ppm) CO₂

levels. The monoculture experiments were used to provide parameters for a resource competition model designed to predict how the species would react to the dynamic changes occurring during growth in the mixed populations.

[Ji et al. \(2017\)](#) showed that at low CO₂, all species were DIC limited, but the performance in terms of the ability to cope with low CO₂ and to compete for HCO₃⁻ ions was *Scenedesmus*>*Chlorella*>*Microcystis*>*Monoraphidium*. At high CO₂, however, population density increased to the extent that cultures became light limited and the competitive capacity was then *Microcystis*≈*Scenedesmus*>*Chlorella*>*Monoraphidium*. When pairs of species were placed in competition at low or high CO₂, the predictions based on the single species cultures were borne out. So at low CO₂, the *bicA* transport system of the *Microcystis* strain did not confer a competitive advantage over the green algae, and at high CO₂ the superior ability of *Microcystis* to cope with the intense shading in dense culture allowed it to outcompete the other species.

Perspectives

It would be interesting to see how the competition between green algae and cyanobacteria would work out with cyanobacterial species/strains expressing higher affinity transporters such as *SbtA* or *BCT1*. The work of [Sandrini et al. \(2016\)](#) and [Ji et al. \(2017\)](#) implies that as the DIC concentrations in the water column change, we are likely to see different strains of cyanobacteria, expressing different transport systems, appearing and disappearing, with strains such as the *Microcystis bicA* strain used by [Ji et al.](#) becoming more dominant as atmospheric CO₂ levels continue to rise. Although past studies have implied that elevated CO₂ is likely to stimulate growth of green algae and other species such as diatoms or Chrysophytes with a lesser (or no) CCM activity (as reflected in internal:external CO₂ concentrations) compared to cyanobacteria, it may well be that instead, all other things being

Box 1. Characteristics of cyanobacterial DIC transporters

Cyanobacterial inorganic carbon transporters differ in affinity and flux rate, and include HCO₃⁻ transporters at the plasmalemma and CO₂ transporters at the thylakoid membrane. Some cyanobacteria can express multiple transporters at the same time or can change expression patterns depending on, for example, external CO₂ levels ([Price, 2011](#); [Sandrini et al., 2015](#)). Expression of different transporters among species and strains will thus confer different physiology and competitive capacity.

Transporter	Substrate	Affinity	Flux	Notes
BCT1	HCO ₃ ⁻	High	Low	ABC-type transporter found exclusively in freshwater β-cyanobacteria; low-CO ₂ inducible
SbtA	HCO ₃ ⁻	High	Low	Sodium-dependent transporter
BicA	HCO ₃ ⁻	Low	High	Sodium-dependent transporter
NDH-1 ₃	CO ₂	High	Low	Energized conversion of CO ₂ to HCO ₃ ⁻
NDH-1 ₄	CO ₂	Low	High	Energized conversion of CO ₂ to HCO ₃ ⁻

equal, we will see a dominance of different cyanobacterial strains filling a succession of niches with varying conditions of alkalinity, pH and $\text{CO}_2/\text{HCO}_3^-$ concentrations. Certainly such niche exploitation by different strains of cyanobacteria is used, for instance, in *Cylindrospermopsis raciborskii* (Burford *et al.*, 2016) and *Microcystis* (Kardinaal *et al.*, 2007) in relation to light availability.

A further complication to note is that CCM expression is not constant (except for constitutive expression of SbtA in the marine α -cyanobacteria such as *Prochlorococcus*; Badger and Price, 2003) and is likely to be modulated by a range of factors including light availability and nutrient levels as well as CO_2 (Beardall and Giordano, 2002; Raven *et al.*, 2011; Raven and Beardall, 2014; Sandrini *et al.*, 2015; Maberly and Gontero, 2017). Thus the competition outcomes in the real world are likely to be much more complicated than the relatively simple systems Ji *et al.* used. Nonetheless, this work is a significant and useful advance in understanding and modelling possible consequences of competition between phytoplankton in a changing environment, and can be complemented by experimental evolution studies to take into account genetic adaptation (Raven and Beardall, 2016; Sandrini *et al.*, 2016).

Key words: Algal blooms, carbon dioxide, climate change, CO_2 -concentrating mechanism, competition model, cyanobacteria, green algae, lakes, *Microcystis*.

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